The 'lawnification' of Australia's eastern grassy woodlands: The past, current and likely future spread of a damaging pasture and lawn grass, Bothriochloa pertusa

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Abstract

Many of today's damaging invasive plants were intentionally introduced for pasture development. By examining the introduction history and consequent spread of these species, we can identify factors associated with their successful establishment and dominance. Using collated presence/absence and cover data, alongside a review of the literature and discussions with land managers, we present a comprehensive analysis of the introduction history and spread of the invasive perennial grass species, *Bothriochloa pertusa* throughout Queensland, Australia. Using this data, we also perform habitat suitability models to predict its potential distribution and local-scale cover across Queensland in relation to key environmental variables. We found that *B. pertusa* was introduced on multiple occasions and across a large area of Queensland, despite re-occurring doubts and poor evidence for its benefit to livestock production. Livestock grazing, associated disturbances (i.e. land clearing, soil erosion) and climatic extremes were commonly associated with its spread throughout the landscape. In 2020 the main area of *B. pertusa* invasion as indicated by occurrence records spanned 28,537,600 ha. Results from the habitat suitability models suggest the occurrence and local-scale cover of *B. pertusa* is largely determined by climate variables and the foliage projective cover of trees. Based on these results *B. pertusa* still has considerable capacity to spread and increase in dominance across many areas of Queensland, particularly further west and south of its current range. The introduction and spread history of *B. pertusa* suggests propagule pressure, traits, climate, land management and cultural perceptions are all key factors implicated in the spread of *B. pertusa*. We recommend more conservative grazing strategies and strategically selected protected areas to slow the spread of this species.

Introduction

The introduction of exotic plant species for the purpose of forage and browse is a pervasive agricultural practice across the globe (Cook, Dias 2006a; Jank et al. 2014; McAlpine et al. 2009; McGill 2015; Walker, Weston 1990). Many of these species become invasive, replacing native pasture species, expanding into natural areas and sometimes transforming ecosystems (Keane, Crawley 2002). Invasive pasture species can lead to changes in plant community composition and diversity either directly, through altered competitive interactions (Firn et al. 2010) or indirectly through changes to ecosystem functions, such as nutrient cycling (Rossiter - Rachor et al. 2009) or fire regimes (Butler, Fairfax 2003; Setterfield et al. 2010). Although the introduction of these species has sometimes improved pasture productivity and led to economic gain (Brenner 2010; Friedel et al. 2011), their success has been variable, with many species achieving negligible benefits for production and instead becoming problematic invasive species (Cook, Dias 2006b; Driscoll et al. 2014; Firn, Buckley 2010; Grice 2006; Setterfield et al. 2010). Despite the impacts of invasive pasture species often being well studied, their introduction history and initial spread is often overlooked or understated within the invasion biology literature (Cook, Dias 2006a; Puth, Post 2005) (but see (Adams et al. 2015)). This is concerning as the introduction and early spread of invaders provide important insights into the mechanisms that drive their expansion and are essential for developing strategies to reduce their spread and impact (Lonsdale 1999). Further, given the pressure to meet global food demands and the potential intensification of pasture development across the globe (Driscoll et al. 2014; McAlpine et al. 2009), having a thorough understanding of historical plant introductions is important for developing appropriate risk assessments for future plant introduction programs. This study presents a comprehensive analysis of the introduction history, spread and potential future distribution of an invasive pasture species, *Bothriochloa pertusa* in Queensland, Australia. We use these findings to propose the key modes of spread for this species and suggest management options. Although the findings presented here are specific to Australia, the methods and concepts are relevant for evaluating and understanding the spread and impact of invaders across the globe.

Methods

2.1 Study species

Bothriochloa pertusa is a perennial stoloniferous grass species native to south-east Asia and India. *B. pertusa* possesses high fecundity and rapid growth rates (Howden 1988; McIvor et al. 1996). *B. pertusa* does not produce high above-ground biomass but forms a dense mat of stolons that allows for a much more continuous ground cover of culms than is typical of tussock grasses. The network of stolons renders *B. pertusa* resistant to grazing, and it typically increases under heavy stocking rates after colonizing bare ground (McIvor 2007a; McIvor et al. 1982).

B. pertusa was first introduced to northern Queensland, Australia 1939 for pasture and lawn trails. Since its introduction in 1939, the perennial grass species, *B. pertusa* has spread widely and has been observed forming apparent monocultures across large areas of Queensland, Australia (Fig. 1). The continued spread of the species poses a significant threat to native biodiversity and ecosystem function (Koci et al. 2020; Kutt, Fisher 2011; Kutt, Kemp 2012; Lebbink et al. 2021a), in a region already under threat from other invasive species, widespread habitat clearance and other anthropogenic disturbances (McAlpine et al. 2009; Reside et al. 2017). Understanding the past and current extent of *B. pertusa* is crucial for predicting and managing its ongoing spread and impacts on native biota.

2.1 Data sources

B. pertusa presence/absence records were collated from multiple data sources and used to describe and analyse the introduction history and spread of *B. pertusa*, and to predict its future distribution throughout the north-eastern Australian state of Queensland. Data included both publicly available records and records collated from field surveys (Table 1, Appendix 1). Once collated, the data was checked, and duplicate records removed. In total we collated 1449 presence records spanning 1939–2019. In addition, 759 contemporary absence records were collated from where *B. pertusa* was not recorded during comprehensive floristic surveys conducted between 2017 and 2020.

For 1262 of the 2208 total presence/absence records, a measure of *B. pertusa* cover was also recorded, either as a percentage or within the broad cover categories (1 = absent, 2 = < 1%, 3 = 1–10%, 4 = 10–20%, 5 = 20–50%, 6 = > 50%). We converted all records to broad cover categories for use in the habitat suitability model described below.

Table 1

Total number of *B. pertusa* presence, absence and cover records collated from a variety of data sources between 1941–2019. Contemporary absence records were collated from where *B. pertusa* was not recorded during floristic surveys conducted between 2017 and 2020. Further information on data collection methods can be found in Appendix 1.

Source	Presence/absence	Cover	Date range
Detailed floristic surveys			
Queensland Herbarium CORVEG	774	738	1984–2019
Other Queensland Herbarium survey sites	411		1950–2019
Department of Agriculture and Fisheries Q-graze	79		1992–2001
Bothriochloa pertusa impact and spread surveys*	130	130	2017–2020
Online sources			
Australian Virtual Herbarium	271		1941–2018
Other			
Bothriochloa pertusa spread surveys*	390	357	2017–2020
Property evaluation vegetation maps**	153		1950–1997
Total	2208	1225	
*Conducted by the author (G. Lebbink) (methods Appendix 1)			
**Sourced from the Queensland Department of Natural Resources, Mines and Energy			

2.2 Introduction history and spread

We used only the *B. pertusa* presence records, alongside information obtained from within the literature, and discussions with land managers to assess and describe the introduction history and spread of *B. pertusa* throughout Queensland. To illustrate its spread, we mapped the change in the total number of presence records (within 30 km grid cells) over time. We calculate the approximate area of invasion using a polygon around the main centroid of occurrence points. This is likely an underestimate of its true range but highlights the area it is most likely to occur.

We acknowledge that there are limitations to using species presence records to discuss trends in a species' spread. In particular, the rate of species collections is not consistent over time and space. However, the trends in this data were verified by information obtained from the literature and discussions with long-term land holders who have witnessed the spread of *B. pertusa*.

2.3 Habitat suitability and predicted future spread

To assess the relationship between *B. pertusa* and key environmental predictors, and to predict its future spread, we performed two habitat suitability models (HSM); one with presence/absence (occurrence) and another with cover as the dependent variable. These models predict the potential distribution of *B. pertusa* based on its current occurrence and environmental preferences. For Queensland, the environmental predictors that were consistently mapped and appropriate for inclusion in a HSM were as follows: land-zones (12 classes which summarise soil and geology), rainfall variability, wet-season rainfall, mean temperature during the growing-season (October to April), distance to a waterway, soil clay content, foliage projective cover (FPC) of trees and vegetation clearing index (3 classes; cleared, regrowth, remnant) (Table 2). Gridded climate data (rainfall variability, wet-season rainfall and mean temperature during the growing season) was obtained from Bureau of Meteorology, 2020. Spatial land-zone information (Christian *et al.* 1953; Gunn *et al.* 1967; Story *et al.* 1967; Speck *et al.* 1968; Galloway, Story & Gunn 1970; Galloway *et al.* 1974; Nix & Gunn 1977) and other environmental data were obtained from the Queensland Government Spatial Catalogue 2020. Land zone 1 which represents tidal flats and beaches was not well represented by the data and was excluded from both the cover and occurrence models. To ensure the cover models were representative of the current invasion potential, only records (both presence and absence) from the last 5 years (2015–2020) and those with a cover value > 20% (as this still reflects vulnerable habitat), were included (1226 records in total). After these data checks, 1433 presence records and 740 absence records (2174) were used in the occurrence models, and 466 presence (with broad cover 2–6) and 760 absence (with broad cover = 1) records were used in the cover model.

A boosted regression tree approach with ten-fold cross validation of training data (Elith et al. 2008) was used to build the HSMs. The resulting occurrence model explained 45% of cross-validated deviance, while the cover model explained 38%. The fitted HSM was used alongside the mapped grids of environmental conditions to predict the probability of occurrence and likely cover of *B. pertusa* within Queensland. Analyses were conducted in R (version 2.10.0, R development Core Team, 2009) using the “gbm” library supplemented with functions from Elith et al. (2008) (see Appendix 2 for full modelling methods).

Table 2
Details of environmental predictors used in habitat suitability models (HSM) to predict *B. pertusa* cover and occupancy.

Variable	Abbreviation	Source	Details
Mean growing season temperature (C°)	MGST (C°)	Bureau of Meteorology (2018)	The mean temperature between October and March based on the standard 30-year period 1961–1990. Data accuracy dependent on available station data. Station data has an accuracy of the order of 0.01 degrees.
Foliage protective cover (%)	FPC (%)	State of Queensland (2021a)	Foliage projective cover is a metric of vegetation cover from the mid- and over-story measured using remotely sensed data sourced from Sentinel2.
Distance to watercourse (m)	DTW (m)	State of Queensland (2021b)	The definition of a watercourse here is any natural channel along which water may flow from time to time, so included both permanent and ephemeral streams.
Rainfall variability index (0 - >2)	RVI	Bureau of Meteorology (2018)	Rainfall variability determined using the percentile analysis method. The index of variability is defined as the 90th rainfall percentile minus the 10th rainfall percentile divided by the 50th percentile. Data accuracy dependent on available station data. Station data has an accuracy of the order of 0.01 degrees.
Mean growing season rainfall (mm)	MGSR (mm)	Bureau of Meteorology (2018)	The mean rainfall between October and March based on the standard 30-year period 1981–2010. Data accuracy dependent on available station data. Station data has an accuracy of the order of 0.01 degrees.
Land-zone	Land-zone	Queensland Herbarium (2020)	Land-zones 1 to 12 describe the major geologies and associated landforms. and geomorphic processes in Queensland. Refer to Wilson et al. 2012 for specific details. Land zone 1 is associated with deposits subject to periodic tidal inundation. Due to poor representation of data points within this area this was excluded from the model.
Clay content (%)	Clay content (%)	CSIRO Land & Water (2011)	Clay content 0–30 cm (250 m raster). Data sourced from state and federal soil surveys.
Clearing score (1 or 0)	Clearing score	Queensland Herbarium (2020)	Allocates polygons as uncleared and high-value regrowth or cleared using a combination of satellite imagery (Sentinel2) and ground truthing surveys.

Table 3

Relative importance of environmental variable to models predicting *B. pertusa* occurrence (presence/absence) and cover. Variable are ordered in decreasing order of importance to the occupancy model. Variables assessed were mean growing season temperature (MGST), foliage protective cover (FPC), distance to waterway (DTW), rainfall variability index (RVI), mean growing season rainfall (MGSR), land-zone, clay content (%) and clearing score.

Variable	**Relative importance (%)**	
	Occupancy	Cover
MGST (C˚)	36.6	29.4
FPC (%)	15.3	15.4
DTW (m)	12.5	10.1
RVI	11.6	17.7
MGSR (mm)	9.5	11.5
Land-zone	9.0	9.1
Clay content (%)	3.6	4.5
Clearing score	1.9	1.3

Results

2.1 Introduction history

Key sources of *B. pertusa* introduction were associated with pasture development, rehabilitation, and amenity.

2.1.1. Pasture development

The first Australian Herbarium samples of *B. pertusa* are from Queensland and date back to 1939, where it was introduced to the Commonwealth Scientific and Industrial Research Organisation (CSIRO) Fitzroy Vale research facility, in Rockhampton (See Fig. 2 for place names), and to the agricultural college facility in Gatton. At Fitzroy Vale, *B. pertusa* was trialled within five 40 m^2 plots; two sown with only *B. pertusa* and three with a mixture of *B. pertusa*, six other exotic grass species and the exotic leguminous shrub *Stylosanthes gracilis* (Miles 1949). At conclusion of the trial in 1942, *B. pertusa* was not included amongst the promising species enlisted for wider regional testing. Among the species considered promising were a number that have since spread widely and had substantial negative environmental impacts; namely *Andropogon gayanus* (Rossiter - Rachor et al. 2009; Setterfield et al. 2010), *Chloris* *gayana*, *Cenchrus ciliaris* (Fairfax, Fensham 2000; Jackson 2005), *Melinis multiflora* (van Klinken, Friedel 2017) and *Panicum maximum* (van Klinken, Friedel 2017).

Despite its poor performance in initial trials, *B. pertusa* continued to be introduced and tested across a number of different research facilities across the state. In the early 1950s, *B. pertusa* was being grown for seed at the CSIRO research facilities in Samford and Strathpine, in South-East Queensland. In 1955, the species was introduced at the Department of Agriculture and Fisheries (DAF) research stations in Emerald and Biloela, in central Queensland. In Emerald, *B. pertusa* was noted as "unimpressive for pastures because of its low productivity" (Bisset 1980). In 1978 *B. pertusa* was introduced to the DAF Brian Pastures research facility, near Gayndah, and in the early 1990s *B. pertusa* was included in pasture trails at CSIRO Landsdown station in Townsville (Jones 1997).

Although its value as fodder was contested, during the late 1980s and into the 1990s the species was recommended as a useful fodder crop, particularly in low fertility soils and to sustain high grazing pressure (Partridge, Miller 1991). A survey of 297 commercial beef producers in Queensland during 1996-97, found *B. pertusa* was used for pasture improvement on some properties in the central coastal region and Brigalow Belt North and in the Einasleigh Uplands (Bortolussi et al. 2005).

2.1.2 Rehabilitation

During the 1970s, *B. pertusa* was introduced to a number of regions across Queensland during trials to assess its value for soil conservation (Bisset 1980; Truong, McDowell 1985). *B. pertusa* was initially trialled for this purpose in research facilities in south-eastern Queensland (Amberley) (Truong and McDowell 1985). This trial led to a series of larger trials in 1979 and 1980 in south, central and northern Queensland, to evaluate the effectiveness of *B. pertusa* in stabilising farm waterways (Truong, McDowell 1985). *B. pertusa* was quick to germinate and establish high cover and deemed useful for stabilising the riverbanks and reducing water erosion. Its use for other stabilising works such as mining overburden and road and railway embankments was also promoted in this study.

During the 1980s the species was sown for mine rehabilitation at Blackwater, Theodore and Callide coal mines near Emerald (Truong, McDowell 1985) and was observed spreading naturally onto mine spoils at the Collinsville coal mine, near Mackay. The abundance of *B. pertusa* on gem-mine spoils in Rubyvale (inland from Emerald) is also likely associated with the rehabilitation of these mines in the late 1990s. It is difficult to determine how frequently the species was used for rehabilitation projects as detailed records were often not kept or were not made available (Silcock 1991). The Queensland Government's Soil Conservation Guidelines (2015), however, suggest that *B. pertusa*, along with *Cenchrus ciliaris* (buffel grass) were used widely for rehabilitation projects on the lighter arid inland soils but "were no longer recommended due their weed potential".

2.1.3 Amenity

The final major source of *B. pertusa* introductions was for amenity purposes, such as lawns, airstrips and along road verges. It was particularly advocated as a lawn species in the drier parts of the state and as such most lawns in central and western Queensland are *B. pertusa* dominant (personal observation, March 4, 2020). Known plantings of *B. pertusa* for amenity in Queensland date to the 1950s with the species recorded as the lawn for the Bowen showgrounds and the airstrips at Cloncurry, Charleville and Bowen aerodromes (Bisset 1980). Sowing of the species for amenity purposes was also occurring in the Northern Territory throughout the late 1980's (Cowie, Werner 1993). Its presence was recorded on the neighbouring Tiwi islands during this time (Fensham, Cowie 1998). The species is now common throughout the Northern Territory and its dominance is increasing in some grazed ecosystems (Robyn Cowley pers. comm. 2019).

2.2 Spread

It wasn't until the mid-1960s that the number of *B. pertusa* herbarium records in Queensland started to increase, and its spread discussed within the literature. During the 1960s *B. pertusa* mostly occurred within the Bowen area, where the species was described to have 'spread like wildfire', during the 1960s and 1970s (Fig. 2a) (Bisset 1980). The landholders of Salisbury Plains, near Bowen first saw the species in 1964 and were 'initially concerned by its aggression' but noted an 'improvement in management and production' in comparison to pastures previously dominated by *Heteropogon contortus* (black spear grass) (Partridge, Miller 1991). Vegetation maps used for property evaluations in the 1960s and 1970s (Table 1, Appendix 1), also suggest the species was dominant across several properties in the Bowen region during this time.

By 1980 the species was observed forming 'solid stands over whole paddocks between the coast and Bogie River', which sits 50 km inland and runs parallel to the coast from Ayr to Bowen (Bisset 1980). The species was also noted as abundant and spreading along roadsides inland from Bowen and up towards Townsville. Transport of hay and cattle from the Bowen region is thought to have facilitated its spread into these regions (Bisset 1980). It was also during the 1980s when *B. pertusa* started to increase in occurrence inland of Mackay, and it is within this region today that *B. pertusa* is particularly abundant (Fig. 2b, e). Coal mining is an extensive enterprise in this region, and the use of *B. pertusa* to rehabilitate mine spoils during this time (Truong, McDowell 1985) is plausibly associated with this spike in occurrences.

Throughout the 1990s the number of records in the Charters Towers region increased considerably (Fig. 2c). *B. pertusa* was observed naturally spreading onto several properties during this time, often from the edge of roads or from neighbouring sown pastures (Bortolussi et al. 2005; O'Reagain, Bushell 2015). A grazing trial initiated in the region in 1992, found a steady increase in *B. pertusa* after the mid-1990s, particularly on heavily grazed sites (Ash et al. 2011). Its increase after this time was suggested to be associated with a series of below average rainfall years prior to 1996, followed by a run of higher rainfall years leading up to the 2000s (Ash et al. 2011). Also during the 1990s, *B. pertusa* was observed replacing substantial areas of *H. contortus* grasslands in central and northern Queensland, with Walker, Weston (1990) suggesting 100,0000 ha in the Burdekin Shire, 200,000 ha in the Dalrymple Shire and 500,000 ha in the Bowen Shire had been colonised by *B. pertusa* by the early 1990s.

During the 2000s the species appeared to expand between Mackay and Charters Towers (Fig. 2d). On a long-term (1998 to current) grazing trial near Charters Towers, the species was very infrequently recorded up until 2007, when it increased exponentially across all grazing treatments, but particularly on the heavily grazed treatments in the poplar box (*Eucalyptus populnea*) woodland (O'Reagain et al. 2022). Similar to the initial spike in the region in the 1990s, this increase on the trial was thought to be associated with the few years of above average rainfall following drought culminating in 2007. The significant increase in *B. pertusa* across the trial was coupled with significant declines in native perennial grass species, particularly of its native congener *Bothriochloa ewartiana*. Also, during the 2000s, *B. pertusa* appeared to increase in the Cape York Peninsula, which aligns with findings from Bortolussi, et al. (2005) who suggest the species was naturally spreading onto several pastoral properties in this region during this time.

In the 10 years between 2010 and 2020 *B. pertusa* continued to spread and increase in dominance in northern and central Queensland, and more recently has spread into southern parts of the state, near Gayndah (Fig. 2e). A producer survey conducted in this region in 2016 suggests that only in the last 5–10 years has *B. pertusa* become particularly noticeable and problematic (Spiegel 2016). Surveys conducted throughout Queensland's grassy woodland ecosystem in 1995-6 across the southern and central Queensland found *B. pertusa* in only 1 of 207 survey sites. We resurveyed 92 of these sites in 2018 and found *B. pertusa* in 43 sites and at greater than 20% cover in nine sites (Lebbink et al. 2022). It's spread within the Gayndah area has likely been even more recent with two producers here suggesting that although it has been present for ~ 25 years (mostly along roadsides) its dominance within the pasture has only become noticeable in the last five years (personal communication, 7 July 2019). Since its introduction to the Brian Pastures research station, near Gayndah, in 1978, *B. pertusa* has also spread considerably, replacing native *Bothriochloa ewartiana* pastures in some areas. In 2020 the key invasion area spanned 28,537,600 ha (calculated from a centroid around main occurrence points).

2.3 Habitat suitability and predicted spread

The occurrence and cover of *B. pertusa* across Queensland was largely predicted by climate (particularly mean temperature during the growing season (October to April)) and FPC of trees (Table 3, Figs. 3 and 4). *B. pertusa* mostly occurred in areas with a mean growing season temperature between 23 C˚ and 27 C˚ and in areas with low tree cover (< 40% FPC). Outside of these thresholds *B. pertusa* was very infrequently recorded. This temperature range is typical of most sub-humid and semi-arid regions of Queensland; as well as in India and south-east Asia, where *B. pertusa* is native.

Where *B. pertusa* was most likely to achieve high cover, was in areas with a mean growing season temperature of 25 C˚ and in areas with < 10% FPC. Its dominance at this temperature may be in part associated with high germination success, with Howden (1988) finding 80% germination at 25 C˚, compared to only 10% at 20 C˚ and 30 C˚. These results align with most other plant species distribution models, which find climate rather than soil or terrain variables, are the most important predictors of plant species occupancy (Syphard, Franklin 2009). This follows that landzone was not highly influential in predicting the occurrence of *B. pertusa*. *B. pertusa* can indeed occur across a wide range of land zones including clay to sandy soils. Although, it is not likely to occur across extremely weathered infertile substrates such as those which occur in the far west of the state. It is also well established that competition from trees (for light and nutrients) limits grass growth, particularly for shade intolerant species, such as *B. pertusa* (Jackson, Ash 1998; Setterfield et al. 2005).

For *B. pertusa* cover, rainfall variability was also a strong predictor, with high cover associated with moderate to high rainfall variability (index of variability ~ 1.0) (Table 3, Fig. 4). This response aligns with anecdotal reports suggesting *B. pertusa* increases after cycles of drought, followed by a period of above average rainfall. Although *B. pertusa* is not considered particularly drought tolerant, its stoloniferous growth strategy and large seed bank enables it to quickly regain space and resources in response to improved growing conditions (Ash et al. 2011; Howden 1988). Conversely, many co-occurring native perennial grass species are considered drought tolerant. Livestock grazing severely compromises this tolerance however, with many studies finding a decline in basal area and survival of native grass species during drought, particularly on intensely grazed sites (Ash et al. 2011; McIvor 2007; Orr, Reagain 2011). Even in response to improved growing conditions, the rate of recovery and recruitment of native grass species was low, and they were often replaced by *B. pertusa* (Ash et al. 2011). Thus, drought and grazing-induced competitive release, combined with the colonising ability and high grazing tolerance of *B. pertusa*, provides the ideal conditions for its proliferation.

Based on habitat suitability, *B. pertusa* still has considerable capacity to spread into new areas of Queensland and to increase in dominance within the coastal and sub-coastal regions where it already proliferates. In particular, it may become more prevalent in the western (towards Longreach and Charleville) and south-western (west from Gayndah), where it has not commonly naturalised (Fig. 5). It is not predicted to reach high cover in these areas however, because these regions are mostly outside the optimal temperature and rainfall range for high *B. pertusa* cover (Fig. 5). Where it already occurs in western Queensland, these limitations to growth have been observed; for instance, on a conservation property near Longreach, *B. pertusa* is common but restricted to seasonally inundated and water run-on areas, suggesting the moister and perhaps cooler microclimates of these habitats allow for its establishment. Results from the HSMs also suggest *B. pertusa* is more likely to occur and achieve high cover closer to waterways (Table 3, Fig. 5.). In southern eastern areas of Queensland, a combination of lower and less variable rainfall and high FPC in many areas has resulted in smaller and more dispersed patches of predicted suitable habitat, and lower predicted cover, than in northern Queensland. Predicted increases to temperature and rainfall variability under future climate change scenarios (IPCC, 2020) may change these range predictions for *B. pertusa*. Likewise, *Cenchrus ciliaris* (Martin et al. 2015) and other tropical exotic grass species (Gallagher et al. 2013), are expected to move southwards with the warmer winter temperatures predicted under climate change.

The predicted extent of *B. pertusa* presented here is based on environmental variables alone. As this paper has highlighted however land management, particularly grazing management is also a very important predictor of spread and dominance in this species. These habitat suitability models should be used in conjunction with information on land management to predict invasion risk more accurately.

2.4. Key learnings and recommendations

Using a combination of empirical and anecdotal data this paper describes the introduction and spread of a damaging invasive species *Bothriochloa pertusa* into Australia. By taking this approach we have gleamed important insights into both the environmental and societal factors involved in the spread of invasive plant species. We have distilled these learnings and propose five key factors associated with the spread for *B. pertusa*: propagule pressure, species traits, land management, climate, and cultural perception. Briefly we discuss each of these factors in turn before providing recommendations for their management.

As this paper highlights, *B. pertusa* was repeatedly introduced across Queensland, sometimes with significant propagule load per dispersal event (such as where it was deliberately sown for pasture or lawn). As a result, propagule load for this species has been far greater than what could have been achieved by natural processes of dispersal. *B. pertusa* is also far more fecund than common co-occurring native species (Howden 1988). High propagule load is a key factor attributed to the success of many invasive plants (Eschtruth, Battles 2009; Fensham et al. 2013; Warren et al. 2013) and it improves the likelihood of a species surviving demographic and environmental stochastic events which threaten small populations (Lockwood et al. 2005).

The physiological traits of *B. pertusa* have potentially provided it an advantage over native species in some contexts. Very few native grasses in Australia are stoloniferous, with most perennial species forming tussocks. Clonality is a trait often associated with invader success as it increases the species capacity to colonise, with options for sexual and asexual reproduction and can provide access to a wider resource pool (Hollingsworth, Bailey 2000; Keser et al. 2014; Wilfried et al. 2012). There is also evidence to suggest *B. pertusa* roots are more resource acquisitive than co-occurring native species (Lebbink et al. 2021a). Indeed, *B. pertusa* recovers rapidly after heavy grazing and drought and this is perhaps associated with these efficient resource acquisition strategies

By opening up space and resources, disturbance can make a ‘weed shaped hole’ for opportunistic invaders to establish (Buckley et al. 2007). The movement of *B. pertusa* across the landscape has been in close association with commercial grazing land uses and associated management practices (including land clearing and fragmentation) (Jones 1997; McIvor et al. 1996; Scanlan et al. 1996). There is also research to suggest the abundance of *B .pertusa* in protected areas, free from domestic grazing, is considerably lower than in adjoining lands grazed by cattle (Lebbink et al. 2021b). The pervasive and wide-spread use of land for intensive grazing systems in Queensland has shifted natural disturbance regimes in favour of *B. pertusa* invasion. Grazing intensity also appears to be important with less *B. pertusa* in areas conservatively grazed (O'Reagain et al. 2022).

The anecdotal and empirical data collated in this paper point to climate and particularly the cycles of drought and heavy rainfall often associated with El Nino and La Nina respectively, as important drivers of *B. pertusa* spread. Drought can reduce the cover of native understorey species and similar to other disturbances creates space and resources for opportunistic species such as *B. pertusa* to monopolise when conditions improve (Diez et al. 2012; Shea, Chesson 2002). Climate has also been associated with the spread of other exotic grasses in Australia including *C. ciliaris* (Buffel Grass) (Fensham et al. 2013) and *Eragrostis curvula* (African Lovegrass) (Roberts et al. 2021). Extreme climatic events can facilitate invasion by a) causing significant and widespread mortality of individuals increasing the available resources for invaders and/or b) reducing the resilience of resident species to respond to improved growing conditions (Diez et al. 2012). Invasion attributed to climate is therefore a factor of the species resilience (both native and invasive), as well as the duration, magnitude and timing of the climatic event (Diez et al. 2012). Understanding how global climate cycles such as La Nina and El Nino affect invasion success is an important area of future research, particularly under an uncertain climatic future.

The early introductions of *B. pertusa* were mostly occurring during a post-war era when there was a big push to develop pastoralism in Australia (Clements, Henzell 2010; Cook, Dias 2006b). Research into the productivity of native pastures was overrun by a campaign for ‘greener pastures’, exotic species bred for high fecundity, productivity and resilience (Cook, Dias 2006b; Driscoll et al. 2014). The aim of some influential agronomists of this time was indeed to replace all existing native pasture species with exotic pasture (Davies 1953). As such, effort to control escaped exotic pasture populations was likely negligible, particularly as this adventive behaviour was considered a good trait of productive pasture (Miles 1949). Thus, exotic pasture species such were *B. pertusa* were given a free pass to invade. Despite their environmental impacts being well known today, these species are in many cases still not considered or managed as ‘weeds’ under government legislations (Department of Agriculture and Water Resource 2017). Exceptions includes species such as *Eragrostis curvula* (African lovegrass) and *Andropogon gayanus* (gamba grass) which are mostly recognised as detrimental to the agricultural industry as well as the (Department of Agriculture and Water Resource 2017). Due to their potential importance economically, exotic pasture species such a *B. pertusa* are ‘taboo weeds’, and this has and continues to stifle attempts to reduce their spread and impact.

Propagule pressure, traits, climate, land management and cultural perceptions are all key factors implicated in the spread of *B. pertusa*. Changing approaches to land management and shifting cultural perceptions may help to improve the management of this species and its consequential spread and impact into the future. Disturbance, whether it be from grazing or drought, and the consequential opening of niche space seems to be an important driver of *B. pertusa* invasion. Ensuring niche gaps are minimal by managing for consistent ground cover may help to reduce the establishment and spread of this stoloniferous species (O'Reagain et al. 2018; O’Reagain, Bushell 2015). Improving grazing management practices to allow adequate rest and rotation of pastures and increasing grazing-protected areas may help to achieve this. This will encourage the persistence of native ground cover and improve the resistance and resilience of ecosystems to stochastic climatic events, and invasion by opportunistic invaders like *B. pertusa*. These approaches may also help to reduce the establishment of monocultures and reduce landscape scale propagule load. Acknowledging environmentally invasive pastures species, such as *B. pertusa* within key state and federal weed legislation is important to both improve public education around these species and to help channel resources into their management.

Conclusion

This study presents a comprehensive analysis of the introduction, spread and potential distribution of an invasive exotic pasture species in Queensland, Australia. By detailing the introduction and spread story of *B. pertusa* we have consolidated and improved our understanding of this species past, current and future distribution and the environmental and cultural factors associated with its spread. Propagule pressure, species traits, land management, climate and cultural perceptions were key factors driving the spread of *B. pertusa*. *B. pertusa* was introduced on multiple occasions and across a large area of Queensland, despite re-occurring doubts and limited evidence of benefit. Its continued spread has been perpetuated by livestock grazing and associated disturbances (i.e., land clearing, soil erosion) and climatic extremes. Results from the HSMs suggest *B. pertusa* will spread and increase in dominance across Queensland particularly in the southern and western parts of the state. We suggest that the use of both empirical and anecdotal information, as has been done in this study, provides a greater depth of understanding than either source alone, and we encourage this approach in future invasion research.

Declarations

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Competing Interests

The authors declare no competing interests.

Author Contributions

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Gabrielle Lebbink. The first draft of the manuscript was written by Gabrielle Lebbink and edited and reviewed by Rod Fensham. All authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

References

1. Adams VM, Petty AM, Douglas MM et al (2015) Distribution, demography and dispersal model of spatial spread of invasive plant populations with limited data. Methods Ecol Evol 6:782–794. https://doi.org/10.1111/2041-210X.12392
2. Ash AJ, Corfield JP, McIvor JG et al (2011) Grazing Management in Tropical Savannas: Utilization and Rest Strategies to Manipulate Rangeland Condition. Rangel Ecol Manage 64:223–239. https://doi.org/10.2111/rem-d-09-00111.1
3. Bisset W (1980) Indian bluegrass has special uses. Qld agricultural J 106:507–517
4. Bortolussi G, McIvor JG, Hodgkinson JJ et al (2005) northern Australian beef industry, a snapshot. 1. Regional enterprise activity and structure. northern Australian beef industry, a snapshot. Reg Enterp activity Struct 45 1:1057–1073
5. Brenner JC (2010) What Drives the Conversion of Native Rangeland to Buffelgrass (Pennisetum ciliare) Pasture in Mexico's Sonoran Desert?: The Social Dimensions of a Biological Invasion. Hum Ecol 38:495–505. https://doi.org/10.1007/s10745-010-9331-5
6. Buckley YM, Bolker BM, Rees M (2007) Disturbance, invasion and re-invasion: managing the weed-shaped hole in disturbed ecosystems. Ecol Lett 10:809. https://doi.org/10.1111/j.1461-0248.2007.01067.x
7. Bureau of Meteorology (2018) Climate Statistics for Australian Locations. Bureau of Meteorology. Australian Government. Available at: http://www.bom.gov.au. (Accessed 20 January 2021)
8. Butler DW, Fairfax RJ (2003) Buffel grass and fire in a gidgee and brigalow woodland: A case study from central Queensland. Ecol Manag Restor 4:120–125. https://doi.org/10.1046/j.1442-8903.2003.00146.x
9. CSIRO Land & Water (2011) ASRIS Australian Soil Classification - Dominant Soil Order (250m raster). Canberra, Australia
10. Clements RJ, Henzell EF (2010) Pasture research and development in northern Australia: an ongoing scientific adventure. Trop Grasslands 44:221–230
11. Cook GD, Dias L(2006a) It was no accident: deliberate plant introductions by Australian government agencies during the 20th century. It was no accident: deliberate plant introductions by Australian government agencies during the 20th century 54:601–625
12. Cook GD, Dias L (2006b) It was no accident: deliberate plant introductions by Australian government agencies during the 20th century. Aust J Bot 54:601–625. https://doi.org/https://doi.org/10.1071/BT05157
13. Cowie ID, Werner PA (1993) Alien plant species invasive in Kakadu National Park, tropical Northern Australia. Biol Conserv 63:127–135. https://doi.org/10.1016/0006-3207(93)90500-Z
14. Davies JG (1953) Research reveals a new Australia. Rural Res 3:2–7
15. Department of Agriculture and Water Resource 2017 Australian Weeds Strategy 2017–2027. Invasive Plants and Animals Committee. Canberra, Australia

16. Diez JM, D'Antonio CM, Dukes JS et al (2012) Will extreme climatic events facilitate biological invasions? Front. Ecol Environ 10:249–257. https://doi.org/https://doi.org/10.1890/110137
17. Driscoll DA, Catford JA, Barney JN et al(2014) New pasture plants intensify invasive species risk. Proceedings of the National Academy of Sciences 111:16622–16627 https://doi.org/10.1073/pnas.1409347111
18. Elith J, Leathwick JR, Hastie T (2008) A working guide to boosted regression trees. J Anim Ecol 77:802–813
19. Eschtruth AK, Battles JJ (2009) Assessing the relative importance of disturbance, herbivory, diversity, and propagule pressure in exotic plant invasion. Ecol Monogr 79:265–280. https://doi.org/10.1890/08-0221.1
20. Fairfax RJ, Fensham RJ (2000) The effect of exotic pasture development on floristic diversity in central Queensland, Australia. Biol Conserv 94:11–21. https://doi.org/10.1016/S0006-3207(99)00169-X
21. Fensham RJ, Cowie ID (1998) Alien plant invasions on the Tiwi Islands. Extent, implications and priorities for control. Biol Conserv 83:55–68. https://doi.org/10.1016/S0006-3207(97)00043-8
22. Fensham RJ, Donald S, Dwyer JM (2013) Propagule pressure, not fire or cattle grazing, promotes invasion of buffel grass Cenchrus ciliaris. J Appl Ecol 50:138–146. https://doi.org/10.1111/1365-2664.12009
23. Firn J, Buckley YM (2010) Impacts of Invasive Plants on Australian Rangelands. Rangelands 32:48–51. https://doi.org/10.2111/RANGELANDS-D-09-00003.1
24. Firn J, MacDougall A, Schmidt S et al (2010) Early emergence and resource availability can competitively favour natives over a functionally similar invader. Oecologia 163:775–784. https://doi.org/10.1007/s00442-010-1583-7
25. Friedel MH, Grice AC, Marshall NA et al (2011) Reducing contention amongst organisations dealing with commercially valuable but invasive plants: The case of buffel grass. Environ Sci Policy 14:1205–1218. https://doi.org/https://doi.org/10.1016/j.envsci.2011.08.001
26. Gallagher RV, Englert Duursma D, O'Donnell J et al (2013) The grass may not always be greener: projected reductions in climatic suitability for exotic grasses under future climates in Australia. Biol Invasions 15:961–975. https://doi.org/10.1007/s10530-012-0342-6
27. Grice AC (2006) The impacts of invasive plant species on the biodiversity of Australian rangelands. Rangel J 28:27–35. https://doi.org/10.1071/RJ06014
28. Queensland Herbarium (2020) Biodiversity status of pre-clearing, 1997 and 2017 remnant regional ecosystems of Queensland series, Version 11.0 (December 2017). State of Queensland (Department of Environment and Science), Brisbane
29. Hollingsworth ML, Bailey JP (2000) Evidence for massive clonal growth in the invasive weed Fallopia japonica (Japanese Knotweed). Bot J Linn Soc 133:463–472
30. Howden M (1988) Some aspects of the ecology of four tropical grasses, with special emphasis on Bothriochloa pertusa. Griffith University, Brisbane

31. Jackson J (2005) Is there a relationship between herbaceous species richness and buffel grass (Cenchrus ciliaris)? Austral Ecol 30:505–517. https://doi.org/10.1111/j.1442-9993.2005.01465.x
32. Jackson J, Ash A (1998) Tree-grass relationships in open eucalypt woodlands of northeastern Australia: influence of trees on pasture productivity, forage quality and species distribution. Int J incorporating Agrofor Forum 40:159–176. https://doi.org/10.1023/A:1006067110870
33. Jank L, Barrios SC, do Valle CB et al (2014) The value of improved pastures to Brazilian beef production. Crop and Pasture Science 65:1132–1137. https://doi.org/https://doi.org/10.1071/CP13319
34. Jones RJ (1997) Steer gains, pasture yield and pasture composition on native pasture and on native pasture oversewn with Indian couch (Bothriochloa pertusa) at three stocking rates. Aust J Agric Res 37:755–765
35. Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends Ecol Evol 17:164–170. https://doi.org/https://doi.org/10.1016/S0169-5347(02)02499-0
36. Keser LH, Dawson W, Song Y-B et al (2014) Invasive clonal plant species have a greater root-foraging plasticity than non-invasive ones. Oecologia 174:1055–1064. https://doi.org/10.1007/s00442-013-2829-y
37. Koci J, Sidle RC, Kinsey-Henderson AE et al (2020) Effect of reduced grazing pressure on sediment and nutrient yields in savanna rangeland streams draining to the Great Barrier Reef. J Hydrol 582:124520. https://doi.org/https://doi.org/10.1016/j.jhydrol.2019.124520
38. Kutt AS, Fisher A (2011) Increased grazing and dominance of an exotic pasture (Bothriochloa pertusa) affects vertebrate fauna species composition, abundance and habitat in savanna woodland. Rangel J 33:49–58. https://doi.org/10.1071/RJ10065
39. Kutt AS, Kemp JE (2012) Native plant diversity in tropical savannas decreases when exotic pasture grass cover increases. Rangel J 34:183–189. https://doi.org/10.1071/rj11048
40. Lebbink G, Dwyer JM, Fensham RJ (2021a) An invasive grass species has both local and broad-scale impacts on diversity: Potential mechanisms and implications. J Veg Sci 32:e12972. https://doi.org/https://doi.org/10.1111/jvs.12972
41. Lebbink G, Dwyer JM, Fensham RJ (2021b) Managed livestock grazing for conservation outcomes in a Queensland fragmented landscape. Ecol Manage Restor 22:5–9. https://doi.org/https://doi.org/10.1111/emr.12460
42. Lebbink G, Dwyer JM, Fensham RJ (2022) ‘Invasion debt’after extensive land-use change: An example from eastern Australia. J Environ Manage 302:114051
43. Lockwood JL, Cassey P, Blackburn T (2005) The role of propagule pressure in explaining species invasions. Trends in ecology & evolution (Amsterdam) 20:223–228. https://doi.org/10.1016/j.tree.2005.02.004
44. Lonsdale WM (1999) Global patterns of plant invasion and the concept of invasibility. Ecology 80:1522–1536. https://doi.org/10.1890/0012-9658(1999)080[1522:GPOPIA]2.0.CO2

45. Martin TG, Murphy H, Liedloff A et al (2015) Buffel grass and climate change: a framework for projecting invasive species distributions when data are scarce. Biol Invasions 17:3197–3210. https://doi.org/10.1007/s10530-015-0945-9
46. McAlpine CA, Etter A, Fearnside PM et al (2009) Increasing world consumption of beef as a driver of regional and global change: A call for policy action based on evidence from Queensland (Australia), Colombia and Brazil. Global Environ Change 19:21–33. https://doi.org/10.1016/j.gloenvcha.2008.10.008
47. McGill B (2015) Land use matters. Nature 520:38–39. https://doi.org/10.1038/520038a
48. McIvor JG (2007) Pasture management in semi-arid tropical woodlands: dynamics of perennial grasses. Rangel J 29:87–100. https://doi.org/10.1071/RJ06031
49. McIvor JG, Singh V, Corfield JP et al (1996) Seed production by native and naturalised grasses in north-east Queensland: effects of stocking rate and season. Trop Grasslands 30:262–269
50. Miles JF (1949) Plant introduction trials in central coastal Queensland 1936-46. Commonwealth Scientific and Industrial Research Organization, Melbourne
51. O'Reagain P, Bushelle J, Pahl L et al (2018) Wambiana grazing trial Phase 3: stocking strategies for improving carrying capacity, land condition and biodiversity outcomes. Meat and Livestock Australia, Sydney
52. O'Reagain PJ, Bushell JJ, Jones P et al(2022) Project B.ERM.0108 Draft final report Wambiana: Grazing strategies and tools to improve profitability and land condition Meat and Livestock Australia, North Sydney, Australia
53. O’Reagain P, Bushell J (2015) Wambiana grazing trial Phase 2: Stocking and spelling strategies for improving carrying capacity and land condition in north Australian grazing lands. Meat and Livestock Australia, Sydney
54. Orr DM, Reagain PJ (2011) Managing for rainfall variability: impacts of grazing strategies on perennial grass dynamics in a dry tropical savanna. Rangel J 33:209–220. https://doi.org/10.1071/RJ11032
55. Partridge IJ, Miller CP (1991) Sown pastures for the seasonally dry tropics. Queensland Dept. of Primary Industries, Brisbane
56. Puth LM, Post DM (2005) Studying invasion: have we missed the boat? Ecol Lett 8:715–721. https://doi.org/10.1111/j.1461-0248.2005.00774.x
57. Reside AE, Beher J, Cosgrove AJ et al (2017) Ecological consequences of land clearing and policy reform in Queensland. Pac Conserv Biol 23:219–230. https://doi.org/https://doi.org/10.1071/PC17001
58. Roberts J, Singarayer F, van Eddie E et al (2021) Seed longevity and germination in response to changing drought and heat conditions on four populations of the invasive weed African lovegrass (Eragrostis curvula). Weed Sci 69:468–477. https://doi.org/https://doi.org/10.1017/wsc.2021.28
59. Rossiter - Rachor NA, Setterfield SA, Douglas MM et al (2009) Invasive Andropogon gayanus (gamba grass) is an ecosystem transformer of nitrogen relations in Australian savanna. Ecol Appl 19:1546–

1560. https://doi.org/10.1890/08-0265.1

60. Scanlan JC, Pressland AJ, Myles DJ (1996) Grazing modifies woody and herbaceous components of north Queensland woodlands. Rangel J 18:47–57. https://doi.org/10.1071/RJ9960047
61. Setterfield SA, Douglas MM, Hutley LB et al (2005) Effects of Canopy Cover and Ground Disturbance on Establishment of an Invasive Grass in an Australia Savanna. Biotropica 37:25–31. https://doi.org/doi:10.1111/j.1744-7429.2005.03034.x
62. Setterfield SA, Rossiter-Rachor NA, Hutley LB et al (2010) Biodiversity Research: Turning up the heat: the impacts of Andropogon gayanus (gamba grass) invasion on fire behaviour in northern Australian savannas. Divers Distrib 16:854–861. https://doi.org/10.1111/j.1472-4642.2010.00688.x
63. Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. Trends in Ecology and Evolution 17:170–176. https://doi.org/10.1016/S0169-5347(02)02495-3
64. Silcock RG (1991) Pastures, trees and shrubs for rehabilitating mines in Queensland: impediments to their use on opencut coal and alluvial mines. Queensland Department of Primary Industries, Brisbane, Queensland
65. Spiegel N (2016) Developing an RD&E project to address loss of productivity in Queensland pastures invaded by Indian couch (Bothriochloa pertusa). Department of Agriculture and Fisheries, State of Queensland
66. Syphard AD, Franklin J (2009) Differences in spatial predictions among species distribution modeling methods vary with species traits and environmental predictors. Ecography 32:907–918. https://doi.org/10.1111/j.1600-0587.2009.05883.x
67. State of Queensland (2021a) Statewide Landcover And Trees Study (SLATS) Sentinel-2–2018 Foliage Projective Cover (FPC) - Queensland. Department of Environment and Science, Dutton Park, Australia
68. State of Queensland (2021b) Watercourse areas – Queensland. Department of Environment and Science, Dutton Park, Australia
69. Truong PN, McDowell M (1985) Indian bluegrass for soil conservation and land stabilization in Queensland. J Soil Conserv Service New South Wales 41:38–43
70. van Klinken RD, Friedel MH (2017) Unassisted invasions: understanding and responding to Australia's high-impact environmental grass weeds. Aust J Bot 65:678–690. https://doi.org/https://doi.org/10.1071/BT17152
71. Walker B, Weston EJ (1990) Pasture development in Queensland - a success story. Trop Grasslands 24:257–268
72. Warren RJ, Ursell T, Keiser AD et al (2013) Habitat, dispersal and propagule pressure control exotic plant infilling within an invaded range. Ecosphere 4:1–12. https://doi.org/10.1890/ES12-00393.1
73. Wilfried T, Núria G, Joan P et al (2012) Ecological niche and species traits: key drivers of regional plant invader assemblages. Biol Invasions 14:1963–1980. https://doi.org/10.1007/s10530-012-0206-0

Figures

Figure 1

Bothriochloa pertusa; a) seed heads, b) stoloniferous life-form, c) example of invasion front in central Queensland. The bright green prostrate grass is *B. pertusa* and the taller tussock is the native *Bothriochloa ewartiana*. d) An example of woodland heavily invaded by *B. pertusa*.

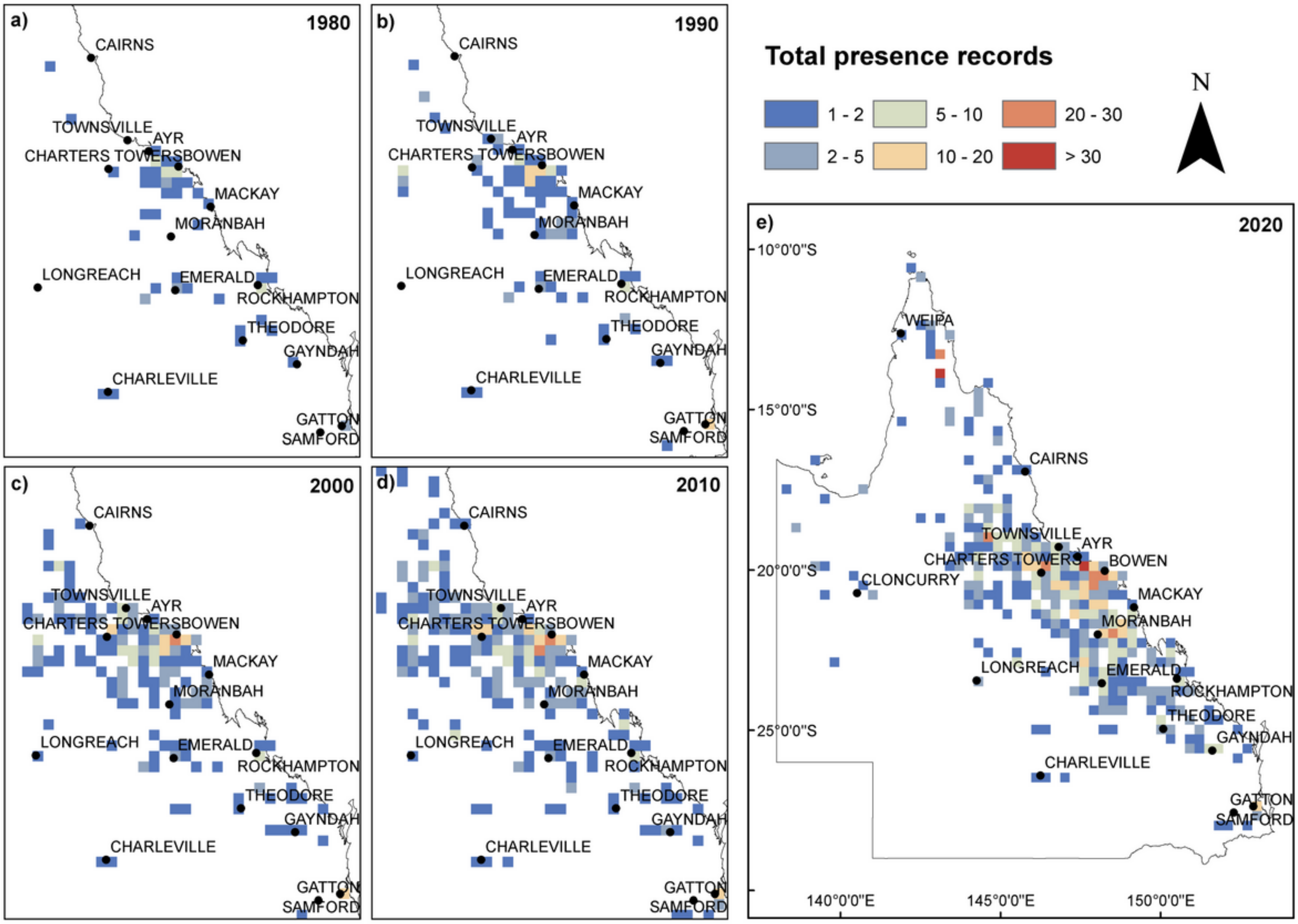

Figure 2

Total *B. pertusa* presence records within 30 km^2 raster grid cells in 1980 (a), 1990 (b) 2000 (c), 2010 (d) and 2020 (e), within Queensland. Records were collated from a number of different data sources which are detailed in Appendix 1.

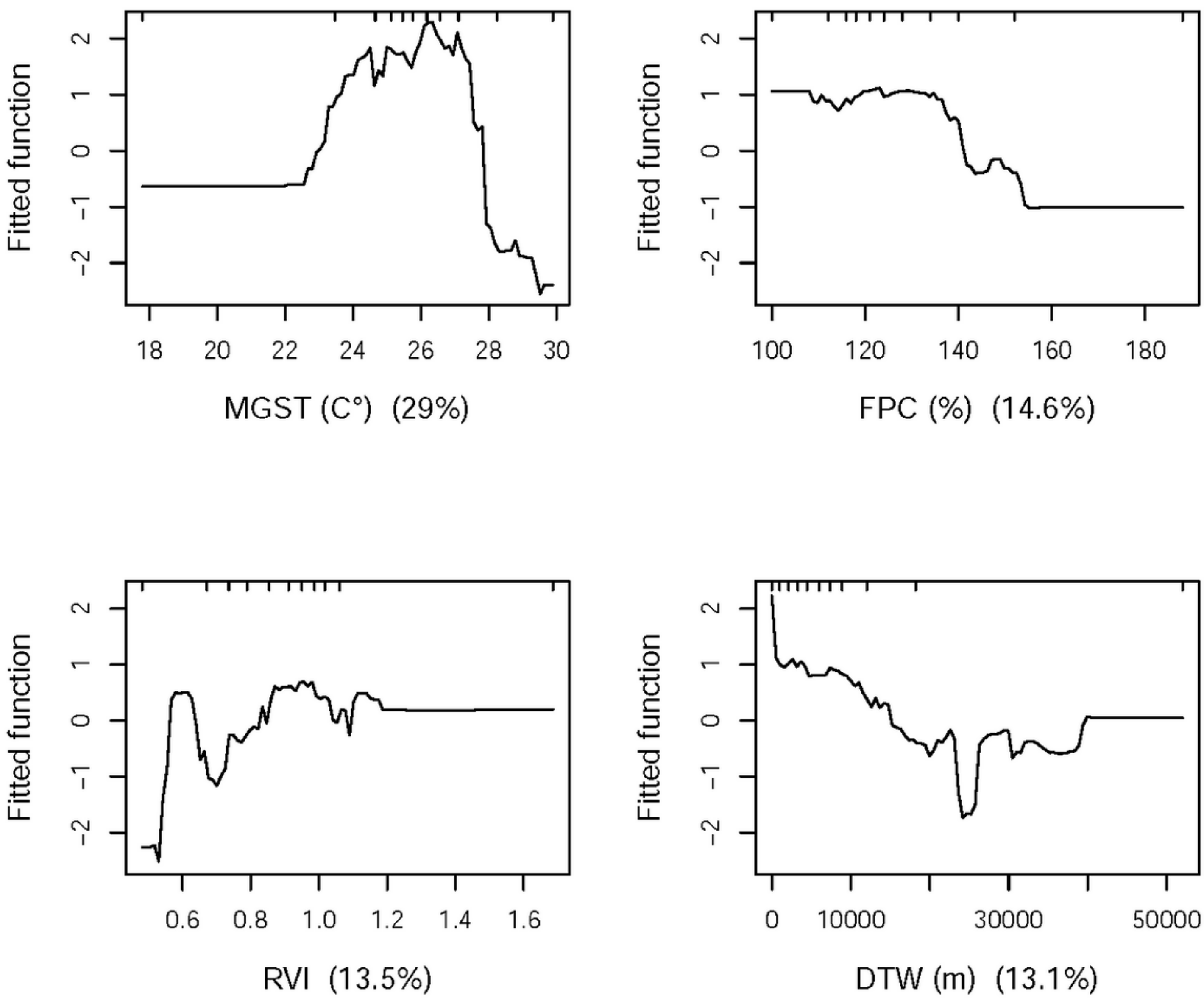

Figure 3

Partial dependence plots for the four most influential variables in the model for *B. pertusa* occurance (presence/absence). Variables are as follows; mean growing season temperature (MGST), foliage projective cover (FPC), rainfall variability index (RVI) and distance to waterway (DTW). Y-axes are on the logit scale and centred to have zero mean over the data distribution. Rug plots at inside top of plots show distribution of sites across that variable, in deciles. See Table 3 for the full list of environmental variables and their relative importance.

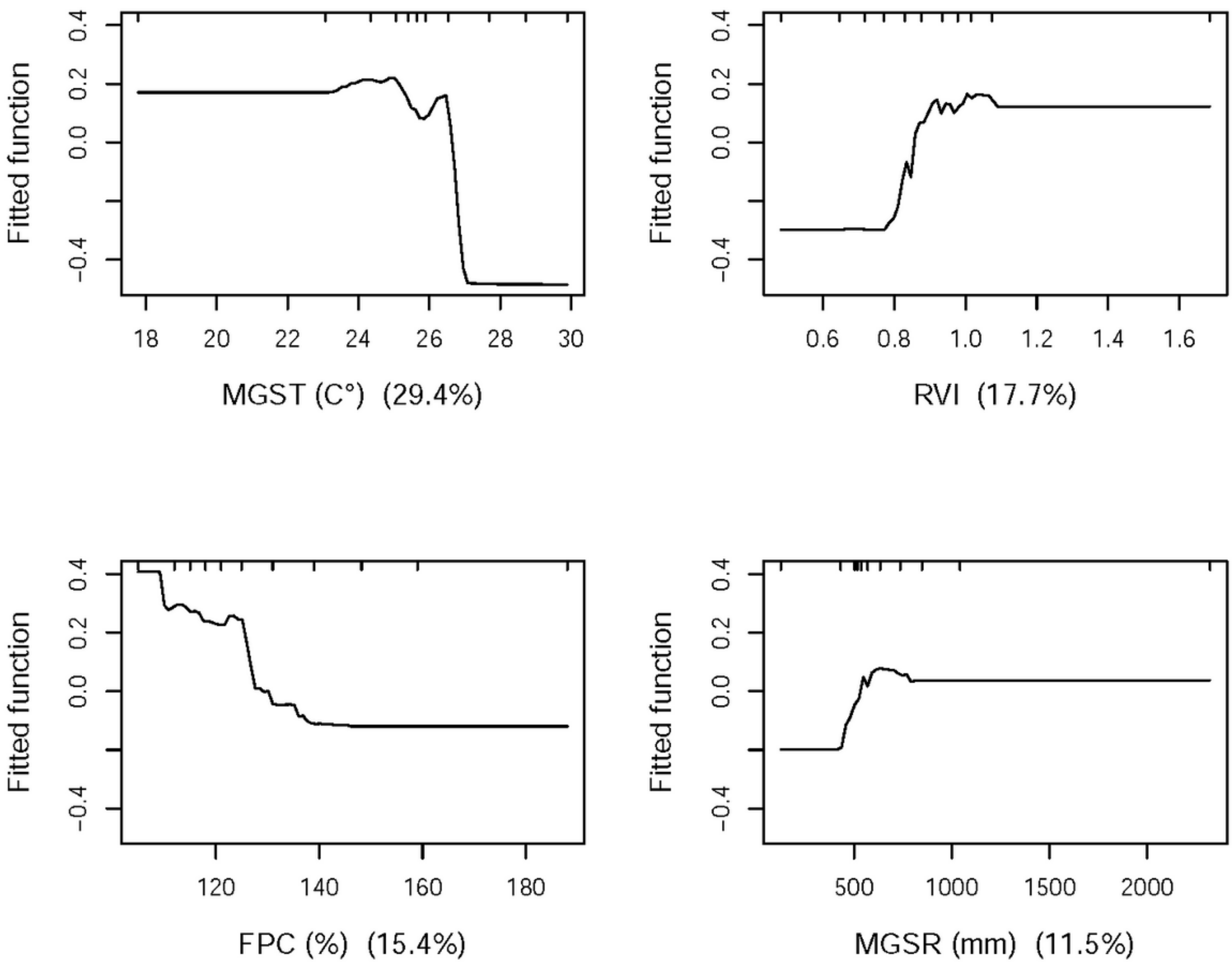

Figure 4

Partial dependence plots for the four most influential variables in the model for *B. pertusa* cover. Variable are as follows; mean growing season temperature (MGST), rainfall variability index (RVI), foliage protective cover (FPC) and mean growing season rainfall (MGSR). Y-axes are on the logit scale and centred to have zero mean over the data distribution. Rug plots at inside top of plots show distribution of sites across that variable, in deciles. See Table 3 for the full list of environmental variables and their relative importance.

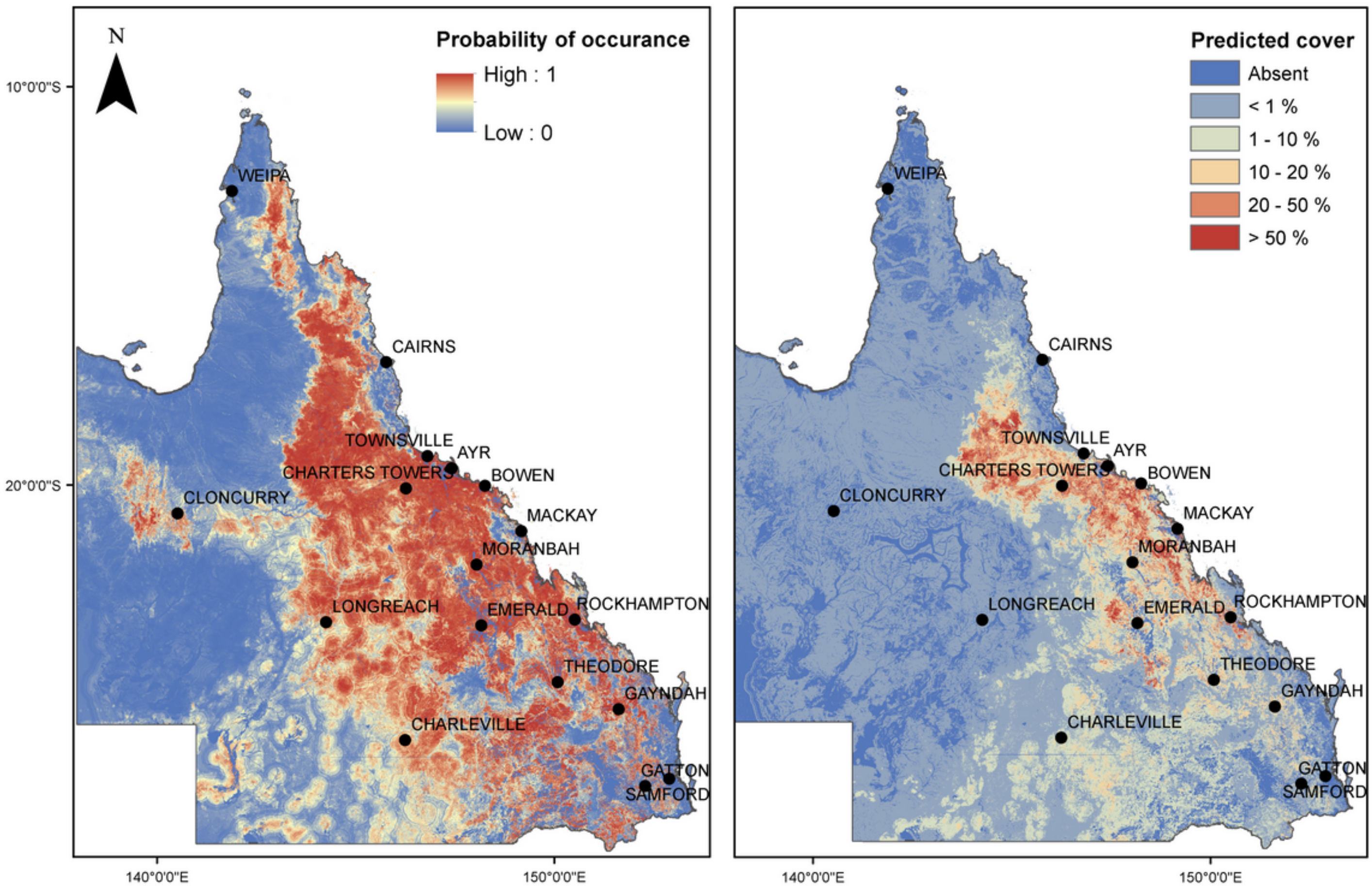

Figure 5

Probability of occurrence (presence/absence) (left) and predicted broad cover (right) of *B. pertusa* in Queensland, as predicted by habitat suitability models, built using boosted regression trees. The resulting occurrence model explained 45% of cross-validated deviance, while the cover model predicted 38%.